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FOOD AND AMPHETAMINE SELF-ADMINISTRATION BY BABOONS: EFFECTS OF ALTERNATIVES

RICHARD W. FOLTIN

NEW YORK STATE PSYCHIATRIC INSTITUTE
AND COLUMBIA UNIVERSITY

The effects of the availability of an alternative reinforcer on responding maintained by food pellets or fluid solutions were examined in 6 adult male baboons (*Papio cynocephalus anubis*). During daily 23-hr experimental sessions, baboons had concurrent access to both food pellets and fluid, with responding maintained under fixed-ratio schedules of reinforcement that varied between the two commodities. The fixed-ratio requirement, or cost, for pellets was increased when (a) no fluid, (b) a dilute dextrose vehicle, (c) 0.002 mg/kg *d*-amphetamine, or (d) 0.004 mg/kg *d*-amphetamine was available. When given nonrestricted concurrent access to food pellets and amphetamine at minimal cost (FR 2), baboons self-administered sufficient amphetamine to decrease pellet intake. Increasing the response requirement for pellets decreased pellet intake at a similar rate regardless of the available fluid and increased fluid intake in a variable manner among baboons such that there were no statistically significant increases in fluid intake. In contrast, when access to pellets was restricted to 70% of maximal intake under nonrestricted conditions, increasing pellet cost decreased pellet intake and increased fluid intake more rapidly when the high amphetamine dose was available. Thus, amphetamine was more effective as an economic substitute for pellets when access to pellets was restricted. The response cost for vehicle and both amphetamine concentrations was increased when baboons had nonrestricted and restricted access to pellets. Increasing the response requirement for fluid delivery decreased intake of all three fluids similarly under both pellet-access conditions. The results indicate that substitution between commodities with minimal commonalities can be studied under controlled laboratory conditions and is dependent upon reinforcement schedule and commodity restrictions.

Key words: food intake, amphetamine, ratio schedules, self-administration, behavioral economics, demand, baboon

Drugs of abuse, as well as reinforcers necessary for life, such as food and water, maintain responding under a wide range of experimental conditions (Johanson & Schuster, 1981). Research with laboratory animals has examined the effects of food availability on drug self-administration (e.g., Carroll & Rodefer, 1993). Among the most robust procedures for increasing drug self-administration, for example, is to maintain laboratory animals at reduced body weight (see review by Carroll & Meisch, 1984). Food deprivation, resulting in decreased body weight, increases the oral and intravenous self-administration of (a) ethanol, which contains calories (Meisch & Thompson, 1973), (b) stimulants with anorectic effects (Carroll & Stotz, 1983), (c) sedatives and anxiolytics with food-intake-increasing effects (Carroll, Stotz, Kliner, & Meisch, 1984), and (d) hallucinogens (Carroll & Stotz, 1984).

The interaction between drug and food self-administration is complex, with changes possible at different points in the chain of behavior leading to drug use. For example, the availability of an alternative reinforcer reduces the rate of acquisition, or initiation, of cocaine self-administration by rats (Carroll, Lac, & Nygaard, 1989). The interactive effects of a nondrug reinforcer on drug self-administration are also influenced by the cost of both commodities and by income (Carroll & Rodefer, 1993). Several authors have turned to the field of behavioral economics to provide a framework for interpreting the effects of nondrug reinforcers on drug intake (Bickel, DeGrandpre, & Higgins, 1995).

The application of economic principles to the experimental analysis of behavior emphasizes the importance of studying responding maintained by a commodity at more than one response requirement or cost (Allison, 1981,

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Reprints may be obtained from the author at New York State Psychiatric Institute, 722 West 168th St., Unit 54, New York, New York 10032.

1983; Hursh, 1980, 1984; Hursh & Bauman, 1987; Lea, 1978). When only one commodity is available, increasing the cost for that commodity will increase responding for that commodity until a cost is reached that maximizes responding. Increasing the cost above that associated with maximal responding will cause responding to decrease below maximal levels. A demand curve can be used to represent the relationship between consumption and cost of the commodity. When responding increases with increasing cost, demand is said to be inelastic, and when responding fails to increase with increasing cost, demand is said to be elastic. The availability of a second commodity can alter the pattern of responding when cost increases for the primary commodity: (a) The second commodity may have no effect on responding for the primary commodity, indicating that the commodities are independent; (b) consumption of the second commodity may decrease as consumption of the primary commodity decreases, indicating that the two commodities are complements; or (c) consumption of the second commodity may increase as consumption of the primary commodity decreases, indicating that the two commodities are substitutes (Green & Freed, 1993; Hursh & Bauman, 1987).

Research from this laboratory has recently been directed toward examining the factors that affect responding maintained by food in baboons. These studies have shown that intake of a caloric alternative (dextrose solution or identical pellets) increases when the cost for food pellets increases. In addition, increases in responding maintained by pellets were significantly smaller when an alternative source of calories was available, that is, demand for food was more elastic in the presence of a caloric alternative (Foltin, 1992, 1994).

Although substitution among commodities can often be predicted by physical characteristics (e.g., different brands of socks, white and whole wheat bread, pens and pencils), even in these cases it is difficult to predict the extent to which one commodity will substitute for another. In many cases, however, even partial substitution among commodities cannot be predicted based upon physical characteristics (e.g., bread and cole slaw). Clearly, most studies involving drug self-administration and an alternative reinforcer fall within this latter category of difficult-to-predict substitution. The economic construct of substitution, based on empirical data, may provide a useful framework for describing such complex interactions among reinforcers (Bickel et al., 1995; Carroll, 1996).

Most studies involving drug self-administration and alternative reinforcers have been designed to examine how the alternative reinforcer, most often the essential commodity, food, affects drug consumption. In the current study, we were interested in how an alternative drug reinforcer affects responding that is maintained by food pellets. The purpose of the present study was to examine how responding for food pellets would be affected by the concurrent availability of an oral amphetamine solution. The interactions between these two commodities were examined when baboons had nonrestricted access to pellets and when access to pellets was restricted. Amphetamine was chosen because it decreases the food intake of laboratory animals and humans (Foltin, 1993; Foltin & Fischman, 1988; Foltin, Kelly, & Fischman, 1990), and it also maintains oral self-administration (Carroll & Stotz, 1983; de la Garza & Johanson, 1987; Jänicke & Coper, 1984). This study provided a parametric evaluation of the ability of self-administered drug and food pellets to function as economic substitutes for each other, and it provided data on the extent to which such substitution was dependent upon food-access conditions.

METHOD

Animals and Apparatus

Six adult male baboons (*Papio cynocephalus anubis*), initially weighing 24.4 to 47.0 kg, were housed in standard primate cages (0.94 by 1.21 by 1.52 m high) at The New York State Psychiatric Institute. The baboons had 3 to 5 years experience responding under fixed-ratio (FR) schedules of food and fluid delivery. The room was illuminated with fluorescent lighting from 6:00 a.m. to 6:00 p.m. daily. In addition to food and fluid earned during experimental sessions, two chewable vitamins (Kiddy Chews, Schein Pharmaceutical, Inc.), two pieces of fresh fruit (80 to 100 kcal each), and a dog biscuit (150 kcal, Old Mother Hubbard, Inc.) were also given daily. Water was available ad libitum from a spout located at the back of each cage. A response panel holding, from bottom to top, a food hopper, two Lindsley levers spaced 0.3 m apart (Gerbrands), four stimulus lights (two above each lever), a fluid spout, and a pellet dispenser (BRS-LVE Model PDC-005) was attached to the front of each cage. Resting on a shelf atop each cage were a 4-l bottle for fluid solutions and a peristaltic pump (7543-06 with pump head 7016 resulting in a flow rate of 10 ml/min; Cole Parmer Instrument Co.). All schedule contingencies were programmed using Apple® IIgs computers located in an adjacent room.

Reinforcement Schedule

Responding on the lever to the baboon's right was maintained by food delivery (Noyes Formula L banana-flavored 1-g food pellets containing 3.7 kcal/g, 21.0% protein, 4.7% fat, 62.0% carbohydrate, 5.3% ash, 3.1% moisture, and 3.0% fiber) under an FR schedule. Responding on the lever to the baboon's left was maintained by delivery of a dilute dextrose solution (D-(+)-glucose, 0.625 or 1.25 kcal per delivery; Sigma) that in some conditions contained *d*-amphetamine sulfate (0.002 or 0.004 mg/kg per delivery; Sigma). Illumination of a red stimulus light above each lever indicated the availability of the commodity associated with that lever. Under the FR schedule, a reinforcer was delivered upon completion of a set number of responses (i.e., lever pulls). A 30-s timeout followed each reinforcer delivery: No stimulus lights were illuminated, and responding, though recorded, had no programmed consequences. Although baboons could respond on either lever at any time, responding did not initiate a new FR until the timeout had elapsed. The first response of a new FR started a limited-hold timer and eliminated the schedule opportunity on the alternate lever. These changes were indicated by stimulus changes on the response panel: The red lights above both levers were extinguished and a green stimulus light was illuminated above the chosen lever. If the response requirement was not completed during the limited-hold period (which varied with the response requirement: FR value × 10 s), the 30-s timeout was initiated and the ratio was reset. The schedule was in effect 23 hr per day, 7 days per week, from 10:00 a.m. to 9:00 a.m. the following morning, except as described below when pellet intake was restricted. The remaining hour of the day was used for cage and animal maintenance. During maintenance periods food and fluid spillage was noted. Spillage is rare with baboons, who nearly always consume delivered items.

Initially, the FR requirement for both commodities was two responses, resulting in the delivery of a 1-g food pellet or 5 ml of fluid. The response requirement was increased, in ascending order, for one commodity on Mondays, Wednesdays, and Fridays, while the other commodity was available under a constant FR 2 schedule. Thus each cost was in effect for 2 or 3 days under each condition. The response cost for pellets was increased until total daily pellet intake decreased to about 190 g (mean pellet intake at minimal cost = 527 g; range, 330 to 768). The response cost for fluid was increased until total daily fluid deliveries decreased to about 10 (mean number of deliveries at minimal cost = 121; range, 20 to 246). Responding for pellets was maintained under FR 2, 16, 32, 64, 128, and 160 schedules, and responding for fluid was maintained under FR 2, 8, 16, 32, 64, and 128 schedules. Given that the maximal FR value was dependent upon each baboon's behavior, the maximal values varied slightly among baboons (Table 1).

Procedure

Responding of each baboon was studied under two pellet-availability conditions. In the first condition, baboons had nonrestricted access to pellets, and during the second condition, the maximum number of pellets that could be earned each day was limited to 70% of pellet intake under the initial nonrestricted condition. Under each pellet-availability condition, seven pellet-fluid access manipulations were completed. Responding was recorded when baboons had access to (a) only pellets, and the response requirement for pellets was increased; (b) pellets and a dilute dextrose vehicle solution, and the response requirement for pellets was increased; (c) pellets and a low-dose amphetamine solution (0.002 mg/kg), and the response requirement for pellets was increased; (d) pellets and a high-dose amphetamine solution (0.004 mg/kg), and the response requirement for pellets was increased; (e) pellets and a vehicle solution, and the response require-

Table 1

Schedule of conditions and response requirements for each baboon.

	Nonrestricted access to pellets			Restricted access to pellets		
		Fluid			Fluid	
Baboon	Pellet cost	Type	Cost	Pellet cost	Type	Cost
1	FR 2–128	None		FR 2–160	None	
	FR 2	1.25 D[a]	FR 2–64	FR 2–160	1.25 D	FR 2
	FR 2–128	1.25 D	FR 2	FR 2	1.25 D	FR 2–128
	FR 2–128	0.004 A[b]	FR 2	FR 2–160	0.002 A	FR 2
	FR 2	0.004 A	FR 2–128	FR 2	0.002 A	FR 2–128
	FR 2	0.002 A	FR 2–128	FR 2–160	0.004 A	FR 2
	FR 2–128	0.002 A	FR 2	FR 2	0.004 A	FR 2–128
2	FR 2–48	None		FR 2–128	None	
	FR 2–48	1.25 D	FR 2	FR 2	0.625 D	FR 2–64
	FR 2	1.25 D	FR 2–48	FR 2–128	0.625 D	FR 2
	FR 2	0.004 A	FR 2–48	FR 2–128	0.004 A	FR 2
	FR 2–64	0.004 A	FR 2	FR 2	0.004 A	FR 2–128
	FR 2–48	0.002 A	FR 2	FR 2–128	0.002 A	FR 2
	FR 2	0.002 A	FR 2–48	FR 2	0.002 A	FR 2–128
3	FR 2–128	None		FR 2–160	None	
	FR 2–128	1.25 D	FR 2	FR 2–128	0.625 D	FR 2
	FR 2	1.25 D	FR 2–128	FR 2	0.625 D	FR 2–128
	FR 2	0.004 A	FR 2–128	FR 2	0.002 A	FR 2–128
	FR 2–128	0.004 A	FR 2	FR 2–160	0.002 A	FR 2
	FR 2–128	0.002 A	FR 2	FR 2	0.004 A	FR 2–128
	FR 2	0.002 A	FR 2–32	FR 2–160	0.004 A	FR 2
4	FR 2–128	None		FR 2–160	None	
	FR 2	1.25 D	FR 2–64	FR 2–160	1.25 D	FR 2
	FR 2–128	1.25 D	FR 2	FR 2	1.25 D	FR 2–128
	FR 2–128	0.004 A	FR 2	FR 2–160	0.002 A	FR 2
	FR 2	0.004 A	FR 2–128	FR 2	0.002 A	FR 2–128
	FR 2	0.002 A	FR 2–64	FR 2–160	0.004 A	FR 2
	FR 2–128	0.002 A	FR 2	FR 2	0.004 A	FR 2–128
5	FR 2–128	None		FR 2–160	None	
	FR 2	1.25 D	FR 2–128	FR 2	0.625 D	FR 2–128
	FR 2–128	1.25 D	FR 2	FR 2–160	0.625 D	FR 2
	FR 2–128	0.004 A	FR 2	FR 2	0.002 A	FR 2–128
	FR 2	0.004 A	FR 2–128	FR 2–160	0.002 A	FR 2
	FR 2	0.002 A	FR 2–128	FR 2	0.004 A	FR 2–128
	FR 2–128	0.002 A	FR 2	FR 2–160	0.004 A	FR 2
6	FR 2–128	None		FR 2–128	None	
	FR 2	1.25 D	FR 2–64	FR 2	1.25 D	FR 2–64
	FR 2–128	1.25 D	FR 2	FR 2–128	1.25 D	FR 2
	FR 2–128	0.004 A	FR 2	FR 2	0.002 A	FR 2–48
	FR 2	0.004 A	FR 2–128	FR 2–128	0.002 A	FR 2
	FR 2–64	0.002 A	FR 2	FR 2	0.004 A	FR 2–64
	FR 2	0.002 A	FR 2–128	FR 2–128	0.004 A	FR 2

[a] D, dextrose (kcal/delivery).
[b] A, *d*-amphetamine sulfate (mg/kg/delivery).

ment for fluid was increased; (f) pellets and a low-dose amphetamine solution, and the response requirement for fluid was increased; and (g) pellets and a high-dose amphetamine solution, and the response requirement for fluid was increased.

Table 1 lists the order of testing each condition for each baboon and the range of FR values that were tested under each condition. Testing order was systematically varied among baboons. When baboons were first given access to the dextrose vehicle, and whenever the fluid commodity was changed, responding was maintained under an FR 2 schedule of pellet delivery and an FR 2 schedule of fluid delivery for 7 to 10 days to allow fluid intake to stabilize. Following completion of the seven conditions with nonrestricted access to pellets, responding was maintained under an FR 2 schedule of pellet delivery without fluid (except water) available for 2 weeks, providing the baseline intake, on an individual basis, that was used to determine pellet intake under nonrestricted access conditions. The maximum number of pellets that could be earned each day was set to 80% of baseline for 1 month and was then reduced to 70% for 1 month prior to retesting the seven conditions. Once a baboon had earned all his pellets during a session, the red stimulus light above the food lever was no longer illuminated, and responding on the pellet lever had no programmed consequences. Preliminary data obtained with a higher dose of amphetamine than used here (0.008 mg/kg), indicated that some baboons that self-administered this dose would stop eating altogether. In order to insure the baboons' safety, the number of fluid deliveries was initially limited to 120 per day. This was increased to 240 shortly into the study for most baboons, but a protocol error inadvertently left the fluid maximum at 120 for Baboons 4 and 5 under the nonrestricted access condition when the high amphetamine dose was available. Although not reported, three experimental conditions were also examined under the 80% access conditions for Baboons 1, 3, 4, and 5, such that they were maintained under 80% access conditions for about 6 weeks longer than the remaining 2 baboons. Responding was recorded when these baboons had access to (a) only pellets, and the response requirement for pellets was increased; (b) pellets and a dilute dextrose vehicle solution, and the response requirement for pellets was increased; and (c) pellets and a vehicle solution, and the response requirement for fluid was increased.

Data Analysis

Data collected on the 2nd day of each FR condition (3rd day if the FR was changed on Friday) were included in the analysis. Responding and reinforcement were recorded throughout the day, providing each of the following dependent measures under all FR conditions: cumulative intake throughout the day; running rate (responses per second during the time from the first to the last response in the FR); number of started ratios that were not completed within the limited hold; and mean size and number of consumption occasions per day (an occasion was defined as beginning with the first response for a commodity and ending when there was a pause longer than 10 min between reinforcement and the initiation of responding under another FR).

Dependent measures were analyzed using repeated measures analyses of variance with two within-subject factors. The first factor was experimental condition (no alternate, where appropriate; dextrose; low and high amphetamine doses), and the second factor was food or fluid cost (each baboon provided data for five response costs). Separate analyses were conducted under each pellet-access condition for responding when the cost for pellets was increased and for responding when the cost for fluid was increased. Given the large individual differences in pellet and fluid intake, the analyses of the number of reinforcers were also accomplished using data that were converted to proportion of baseline intake under that condition. Results were considered statistically significant at $p < .05$.

RESULTS

Effects of Increasing Pellet Cost on Pellet and Fluid Intake

The top panels of Figure 1 present total daily pellet intake as a function of pellet cost when baboons had restricted and nonrestricted access to pellets and concurrent access to each of the three fluids. Providing baboons with a fluid alternative significantly decreased total pellet intake under nonrestricted access conditions, $F(3, 15) = 20.14$, $p < .0015$. Increasing the cost of each pellet significantly decreased total pellet intake, $F(4, 20) = 20.14$, $p < .0001$. When access to pellets was restricted, total pellet intake was identical under the FR 2 condition. Increasing the cost for pellets significantly decreased total pellet intake, $F(4, 20) = 16.17$, $p < .0001$. There was a significant main effect of fluid condition on total pellet intake, $F(3, 15) = 27.31$, $p < .003$, and a significant Condition × Cost interaction, $F(12, 60) = 2.00$, $p < .039$. Contrasts indicated that total pellet intake at maximum cost when the high amphetamine dose was available was less than total pellet intake under either the low amphetamine dose, $F(1, 60) = 8.34$, $p < .011$, or dextrose conditions,

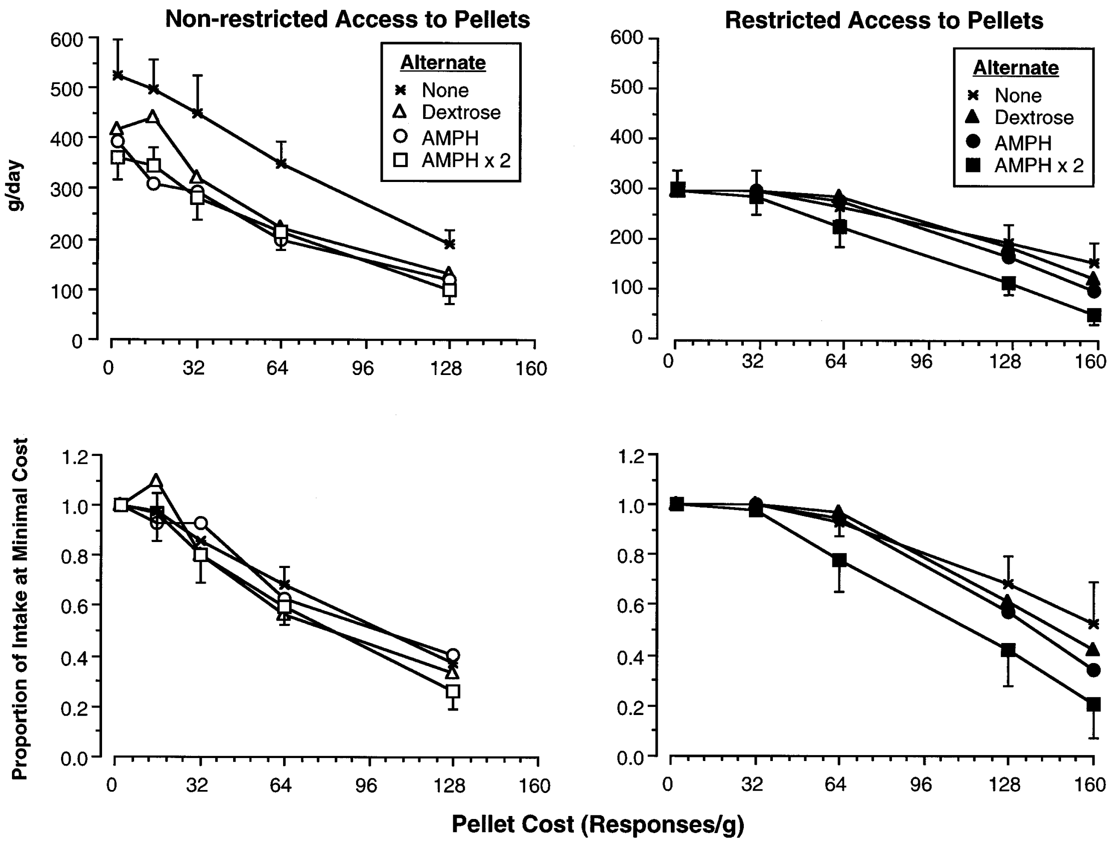


Fig. 1. Mean total daily pellet intake as a function of pellet cost and type of concurrently available fluid when baboons had nonrestricted access to pellets (top left). Mean total daily pellet intake as a function of pellet cost and concurrently available fluid when access to pellets was restricted (top right). Data presented in top panels converted to proportion of intake at minimal cost (FR 2) (bottom). Error bars, representing 1 standard error of the mean (*SEM*), are presented for the no fluid and high amphetamine dose only.

$F(1, 60) = 7.12$, $p < .017$. Clearly, pellet intake decreased more rapidly as cost increased when amphetamine was available and pellet intake was restricted.

Given the variability in baseline pellet intake when access to pellets was not restricted, the data are regraphed in the bottom panels of Figure 1 as a proportion of pellet intake under minimal cost. Converting pellet intake to a proportion of baseline produced curves that overlapped substantially when pellet intake was unrestricted. Although total pellet intake still decreased as cost increased, $F(4, 20) = 50.67$, $p < .0001$, there were no differences among fluid conditions. In contrast, converting pellet intake to a proportion of baseline when pellet intake was restricted did not alter the pattern of results: Pellet intake differed among the four conditions, $F(3, 15) = 7.34$, $p < .003$, decreased with increasing cost, $F(4, 20) = 20.89$, $p < .0001$, and was lower at maximum cost when the high amphetamine dose was available compared to dextrose, $F(1, 60) = 10.16$, $p < .002$.

Figures 2 and 3 present total daily pellet (g) and amphetamine (mg/kg) intake as a function of fluid condition (dextrose vehicle and 0.002 and 0.004 mg/kg amphetamine) and pellet cost for each baboon. The data shown in Figure 2 were obtained when baboons had nonrestricted access to pellets, and the data shown in Figure 3 were obtained when baboons had restricted access to pellets. Because logarithmic scales are commonly used in studies that manipulate response cost, the data in Figures 2 and 3 are graphed using logarithmic scales. Baboons 2, 3, and 5 increased the number of fluid deliveries under

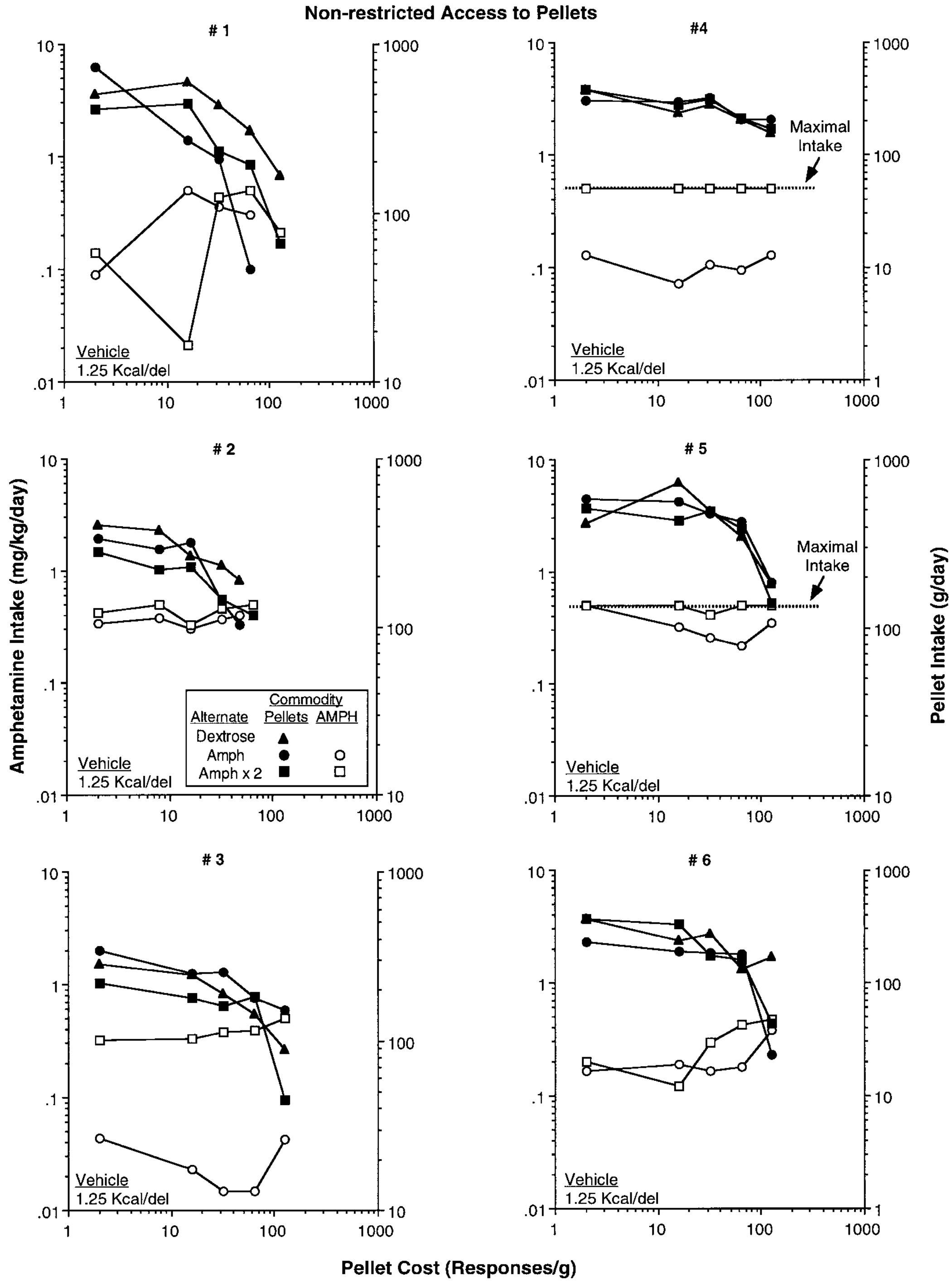


Fig. 2. Total daily amphetamine (milligrams per kilogram; open symbols) and pellet intake (in grams; closed symbols) as a function of pellet cost and amphetamine dose for each baboon under the nonrestricted access condition. A protocol error inadvertently left the fluid maximum at 120, indicated by the dotted line, for Baboons 4 and 5 under the nonrestricted access condition when the high amphetamine dose was available. Note that axes are logarithmic.

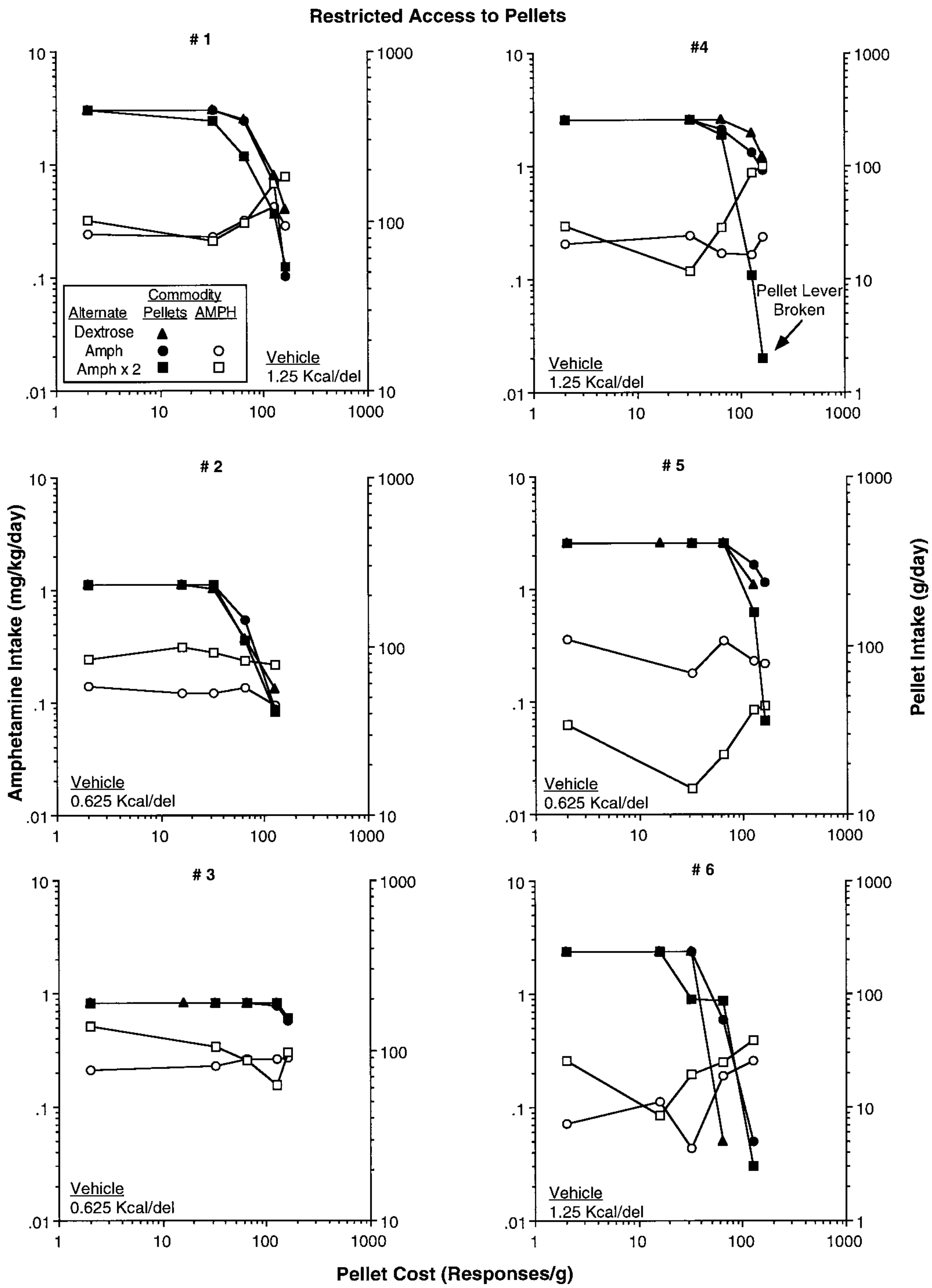


Fig. 3. Total daily amphetamine (milligrams per kilogram; open symbols) and pellet intake (in grams; closed symbols) as a function of pellet cost and amphetamine dose for each baboon when access to pellets was restricted to 70% of baseline under the nonrestricted access condition. Note that axes are logarithmic.

the restricted access condition to the maximum 240 (300 kcal per day, or the equivalent of 81 pellets; data not shown). Because this left no room for possible increases in fluid deliveries under amphetamine conditions, the dextrose concentration was halved (0.625 kcal per delivery), and the maximum number of fluid deliveries was increased to 360. Although this change reduced the number of vehicle deliveries, it complicates comparisons between the two food-access conditions. Examination of the individual data (Figures 2 and 3) indicates that fluid intake increased with increasing pellet cost for some baboons and under some fluid conditions, but the effects were not consistent. In summary, (a) increasing the cost for pellets decreased pellet intake under both food-access conditions, (b) pellet intake decreased more rapidly with increasing cost when amphetamine was available and food intake was restricted, and (c) fluid intake increased for some baboons under some fluid conditions, but the effects varied greatly among baboons.

In order to provide estimates of stability, the range, mean, and median of the number of reinforcers obtained under each FR 2 condition are presented in Table 2. In nearly every case, the mean and median of the distributions are within 10 reinforcers. The minimum number of reinforcers obtained under each FR condition almost always occurred on the 1st day of that condition, except under FR 2 conditions, when the maximum responding usually occurred on the 1st day. Because FR values were tested in increasing order, FR 2 conditions always occurred after the largest FR tested for each baboon. For this reason, data presented in the figures were obtained on the 2nd day of 2-day conditions and the 3rd day of 3-day conditions.

The top panels of Figure 4 present total number of fluid deliveries as a function of pellet cost and fluid condition. The total number of fluid deliveries increased slightly, although not significantly, with increasing pellet cost when baboons had nonrestricted access to pellets: Dextrose intake increased by 13%, and intake of both amphetamine doses increased by 25%. Intake of the high amphetamine dose increased by 63% ($p < .06$) with increasing pellet cost, when baboons had restricted access to pellets, whereas dextrose intake increased by 1%, and intake of the low amphetamine dose increased by 9%. Given the variability in baseline fluid intake, the data are regraphed in the bottom panels of Figure 4 as a proportion of fluid intake under minimal cost. Although fluid intake increased by about 100% to 250% under both pellet-access conditions, there were no significant differences related to either fluid condition or pellet cost.

Effects of Increasing Fluid Cost on Fluid and Pellet Intake

Figure 5 compares total daily amphetamine intake as a function of unit price (i.e., number of responses emitted to obtain 0.002 mg/kg amphetamine) for each baboon when baboons had restricted and nonrestricted access to pellets. Because the same FR values were used for both the low and high amphetamine doses, the unit price for the low dose at each FR value was doubled (i.e., half the amount of drug was delivered following the same number of responses), shifting the curves for the low amphetamine dose to the right of the curves for the high amphetamine dose. The data in Figure 5 are graphed on logarithmic axes and are presented as a function of unit price because such presentations are often used in studies that vary response requirements.

Figure 6 presents the number of fluid deliveries as a function of fluid cost when baboons had restricted and nonrestricted access to pellets and concurrent access to each of the three fluids. These data are presented as number of deliveries per FR value, rather than drug dose each day as a function of amphetamine unit price, because dextrose contained no amphetamine.

When baboons had nonrestricted access to pellets (top middle panel of Figure 6), there were no differences among fluid conditions in intake as a function of cost. Increasing the cost per fluid delivery significantly decreased intake of all three fluids, $F(4, 20) = 10.55$, $p < .0001$. With one exception (Baboon 6), there was no evidence for increased amphetamine intake under the restricted access conditions compared to the nonrestricted condition (although the sweetness of the vehicle was decreased for Baboons 2, 3, and 5). When access to pellets was restricted (top left panel of Figure 6), increasing the cost per fluid delivery significantly decreased intake of

Table 2

Indexes indicating variability in commodity intake when commodities were available under a fixed-ratio 2 schedule of reinforcement (five to eight sessions). Values indicate the number of deliveries per session.

Baboon	Commodity	Nonrestricted access to pellets				Restricted access to pellets			
		Min	Max	Mean	Median	Min	Max	Mean	Median
1	Pellets	597	688	641	652	449	449	449	449
	1.25 kcal/ml dex	38	181	77	59	55	183	134	144
	Amph	47	171	110	117	77	162	125	125
	Amph × 2	25	120	76	70	55	97	77	80
2	Pellets	319	354	332	329	233	233	233	233
	1.25 kcal/ml dex	111	202	166	166				
	0.625 kcal/ml dex					102	141	125	128
	Amph	115	160	136	137	55	100	68	61
	Amph × 2	86	120	111	119	44	75	57	59
3	Pellets	246	306	279	281	191	191	191	191
	1.25 kcal/ml dex	121	198	154	148				
	0.625 kcal/ml dex					88	175	120	108
	Amph	50	66	61	64	89	148	119	116
	Amph × 2	49	104	66	60	72	128	100	100
4	Pellets	331	387	364	364	254	254	254	254
	1.25 kcal/ml dex	151	221	177	180	125	195	151	146
	Amph	31	78	54	52	57	139	113	118
	Amph × 2	92	120	109	110	66	134	87	84
5	Pellets	496	645	580	573	406	406	406	406
	1.25 kcal/ml dex	129	264	217	241				
	0.625 kcal/ml dex					69	124	91	85
	Amph	47	171	110	117	35	210	107	85
	Amph × 2	118	120	119	120	35	103	58	56
6	Pellets	302	379	338	338	237	237	237	237
	1.25 kcal/ml dex	20	67	42	43	25	71	59	63
	Amph	31	80	51	39	34	76	56	54
	Amph × 2	36	65	47	45	32	58	46	48

all three fluids, $F(4, 20) = 60.05$, $p < .0001$. There was a significant interaction between fluid condition and fluid cost, $F(8, 40) = 2.38$, $p < .033$: The number of dextrose deliveries was greater than the number of amphetamine deliveries under the three lower costs, but was lower than the number of amphetamine deliveries under the two higher costs. The bottom panels of Figure 6 present the data contained in the top panels after they were converted and analyzed as proportions of baseline. When analyzed as proportions of baseline, the data confirm the results based on absolute intake: increasing the cost per fluid delivery significantly decreased intake of all three fluids when pellet access was not restricted, $F(4, 20) = 13.13$, $p < .0001$, and when pellet access was restricted, $F(4, 20) = 123.48$, $p < .0001$, and there was a significant interaction between fluid condition and fluid cost when pellet access was restricted, $F(8, 40) = 2.61$, $p < .021$.

The top right panel of Figure 6 compares the total daily number of pellet deliveries among the three fluid conditions as a function of increasing fluid cost when baboons had nonrestricted access to pellets. Contrasts calculated for the Fluid Condition × Cost interaction indicated that pellet intake significantly increased when the cost of the high amphetamine dose was increased, $F(1, 40) = 4.34$, $p < .044$. Converting and analyzing the data as proportion of baseline, as shown in the lower right panel, yielded a borderline nonsignificant effect of cost ($p < .09$) and confirmed that pellet intake increased when the cost of the high amphetamine dose was increased, $F(1, 40) = 8.57$, $p < .0056$. When access to pellets was restricted, pellet intake remained at maximum levels regardless of

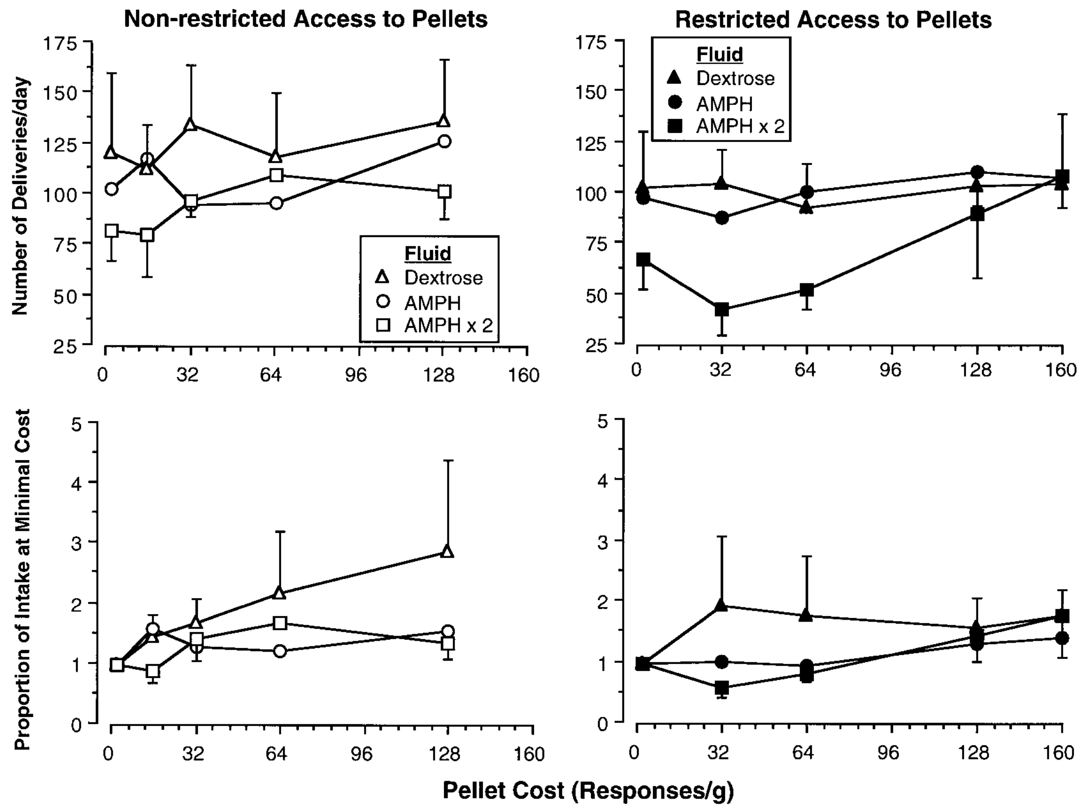


Fig. 4. Mean total number of fluid deliveries as a function of pellet cost and fluid when baboons had nonrestricted access to pellets (top left). Mean total number of fluid deliveries as a function of pellet cost and fluid when access to pellets was restricted (top right). Data presented in top panels converted to proportion of intake at minimal cost (FR 2) (bottom). Error bars, representing 1 *SEM,* are presented for the dextrose and high amphetamine dose only.

fluid cost (data not shown). Thus, increasing the cost per fluid delivery (a) decreased fluid intake under both pellet-access conditions, (b) decreased dextrose intake at a faster rate than amphetamine intake when access to pellets was restricted, and (c) increased pellet intake when access to pellets was not restricted and the high amphetamine dose was available.

Effect of Pellet Cost on the Pattern of Pellet and Fluid Intake

Figures 7 and 8 present cumulative pellet and amphetamine intake as a function of session time and response cost for pellets for a representative baboon under each pellet-access condition. For the most part, the cumulative records show a pattern of eating (meal) or fluid occasions characterized by the consumption of multiple food pellets or fluid deliveries, followed by a pause in responding. Both figures clearly show greater amphetamine intake and reduced pellet intake under the high pellet cost compared to baseline (FR 2). Food restriction greatly altered the pattern of pellet intake, with the majority of pellet intake occurring during the first eating occasion of the day (Figure 8). In contrast to the nonrestricted access condition, in which bouts of pellet and fluid intake occurred in proximity (Figure 7), fluid intake under restricted access conditions did not occur until after the first eating occasion had been completed. Increasing the response requirement for a pellet decreased the latency to the first fluid delivery, an effect most noticeable under the restricted access condition.

Figure 9 presents a comparison of the number of eating occasions and mean eating occasion size as a function of pellet cost under both pellet-access conditions. Under the nonrestricted baseline condition, baboons

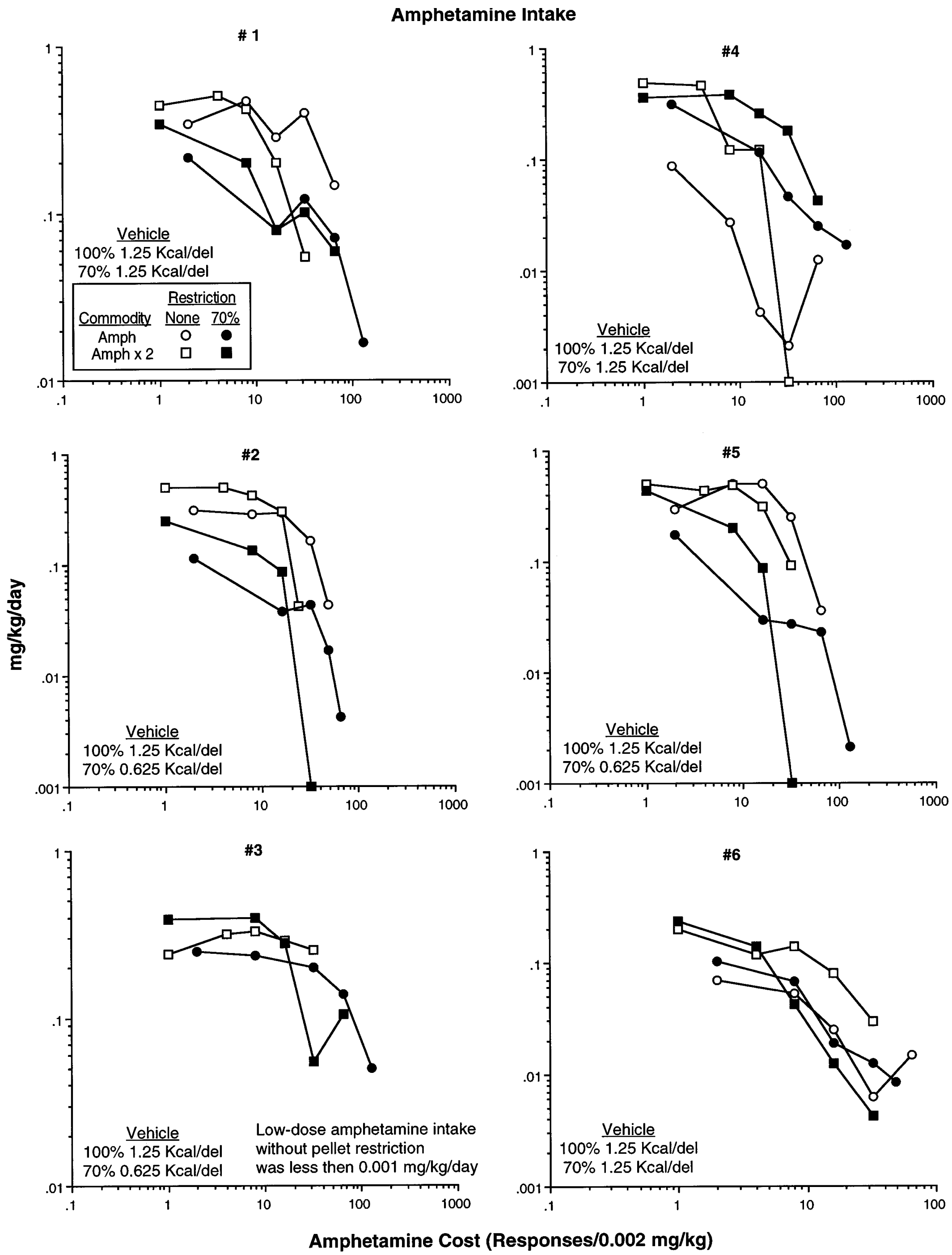


Fig. 5. Total daily amphetamine intake obtained from two concentrations of amphetamine solution (0.002 mg/kg or 0.004 mg/kg) as a function of amphetamine unit price (responses/0.002 mg/kg) under both pellet-access conditions for each baboon. Note that axes are logarithmic.

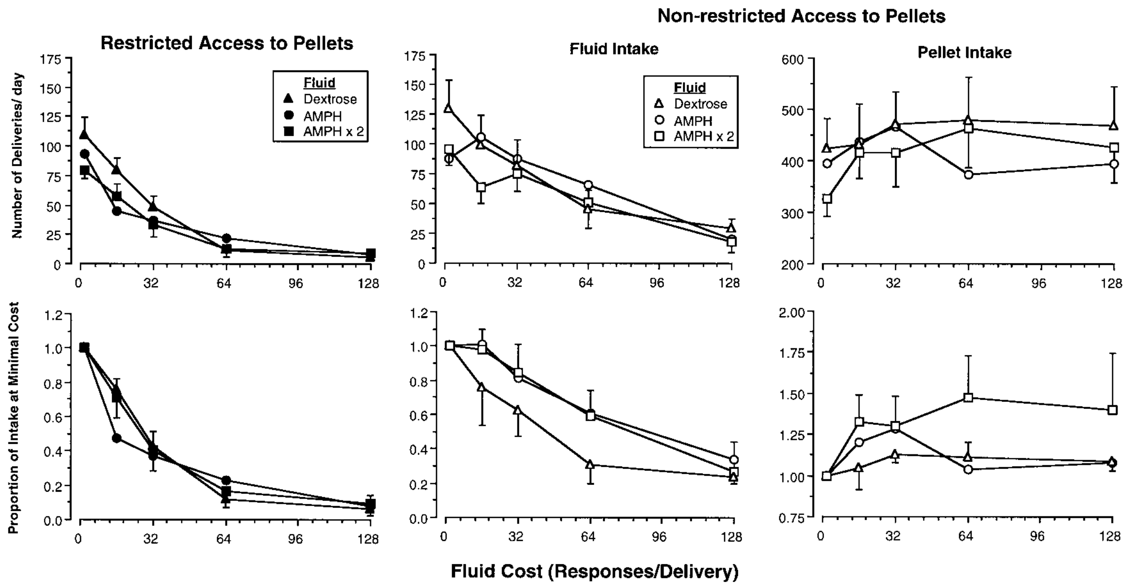


Fig. 6. Mean total number of fluid deliveries as a function of fluid cost and fluid type when access to pellets was restricted (top left). Mean total number of fluid deliveries as a function of fluid cost and fluid type when baboons had nonrestricted access to pellets (top middle). Mean total daily pellet intake as a function of fluid cost when baboons had nonrestricted access to pellets (top right). Data presented in top panels converted to proportion of intake at minimal cost (FR 2) (bottom). Error bars, representing 1 *SEM,* are presented for the dextrose and high amphetamine dose only.

had about 9 to 11 eating occasions per day, each containing about 50 pellets. Increasing the cost per pellet decreased pellet intake by significantly decreasing the mean size of eating occasions, $F(4, 20) = 9.52$, $p < .0002$, without affecting the number of eating occasions. A different pattern of results was observed when access to pellets was restricted. Restricting access decreased the number of eating occasions and increased mean eating occasion size under the FR 2 conditions compared to the nonrestricted conditions. This effect was due to the consumption of most of the pellets in the first eating occasion of the day (see representative data in Figure 8). In contrast to nonrestricted access, increasing the response requirement per pellet delivery significantly increased the number of eating occasions, $F(4, 20) = 9.90$, $p < .0001$, and significantly decreased mean eating occasion size, $F(4, 20) = 10.93$, $p < .0001$.

Running response rate on the pellet lever (data not shown) was four to five responses per second under all pellet-access conditions and fluid conditions when the cost was greater than FR 2 (response rate under the FR 2 schedule was always higher but was not meaningful because the rate could not be accurately determined based on the time between only two responses). Once a baboon initiated a bout of responding, it rarely did not complete the ratio; the number of incomplete ratios varied between only one and five per day, regardless of pellet cost and food-access condition. Thus, when responding resumed after a pause, it continued at a consistent rate until reinforcement occurred. Restricting access to pellets altered both the topography of eating and drinking under baseline conditions and the changes in topography observed when the response requirement for a pellet was increased.

Effect of Fluid Cost on the Pattern of Pellet and Fluid Intake

Figure 9 also presents a comparison of the number of fluid drinking occasions and mean drinking occasion size as a function of pellet cost under both pellet-access conditions. Under the nonrestricted baseline conditions when vehicle was concurrently available, baboons had about 20 drinking occasions per day, each containing about six deliveries, when fluid was available at mini-

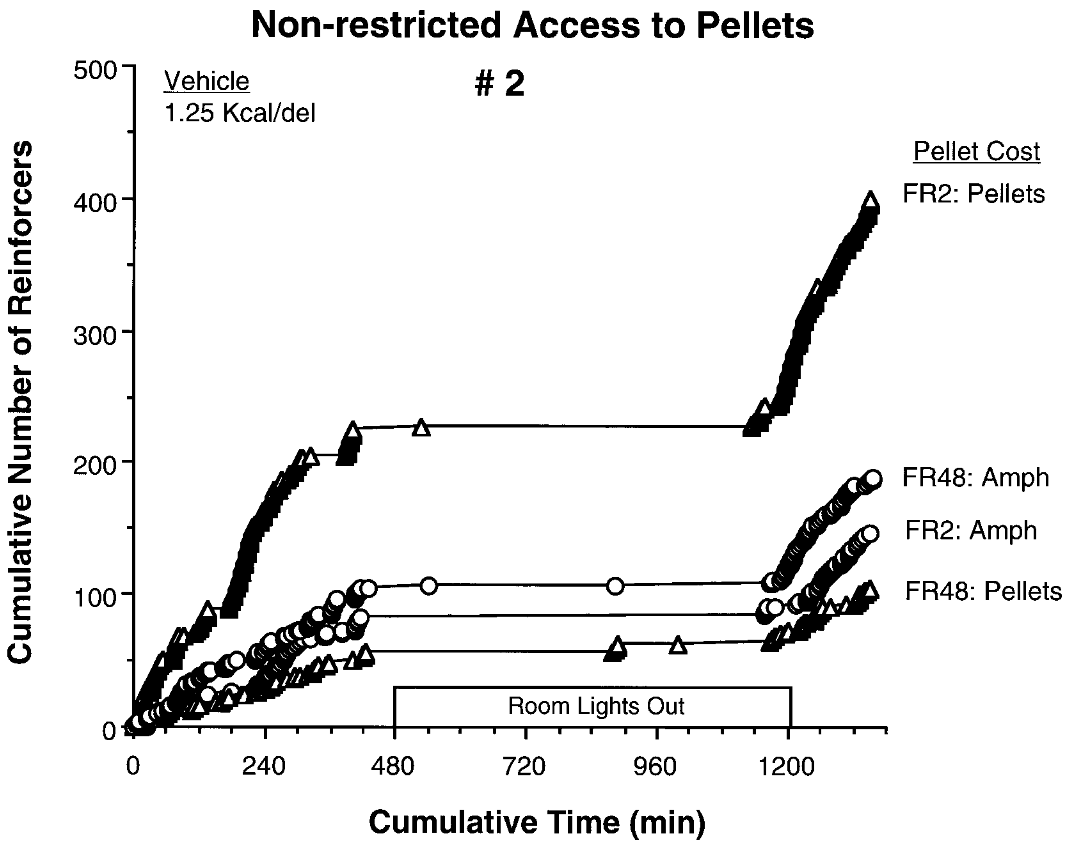


Fig. 7. Cumulative number of pellet and amphetamine deliveries when pellets were available at minimum (FR 2) and maximum cost (responses per delivery) for Baboon 2 (FR 48) when access to pellets was not restricted. Each symbol represents reinforcement, not a response.

mal cost. Increasing the cost per fluid delivery decreased fluid intake by significantly decreasing the mean number of drinking occasions, $F(4, 20) = 7.43$, $p < .0008$, without clearly affecting the size of drinking occasions ($p < .07$).

When access to pellets was restricted, increasing the cost per fluid delivery decreased fluid intake by significantly decreasing the mean number of drinking occasions, $F(4, 20) = 86.73$, $p < .0001$, and significantly decreasing the size of drinking occasions, $F(4, 20) = 8.27$, $p < .0004$. Thus, although increasing the cost for pellets decreased pellet intake by decreasing the size of eating occasions, increasing the cost for fluid decreased fluid intake by decreasing the *number* and size of drinking occasions.

With the exception of baseline conditions, running response rate for fluids was consistent across all fluid costs and available fluid type, and remained between 1.5 and 2.0 responses per second. Once a baboon initiated a bout of responding on the fluid lever, it was rare that a baboon did not complete the ratio; the number of incomplete ratios varied between only one and five per day, regardless of fluid cost or available fluid type. Thus, when responding on the fluid lever resumed after a pause, it continued at a consistent rate until reinforcement occurred.

Body Weight

Table 3 compares the initial starting weight of each baboon with the weight obtained when the first condition was tested under the restricted access condition and when the last condition was tested under the restricted access condition. Over the first half of the study (until the restriction began) 2 baboons lost weight, 3 gained weight, and 1 remained at the same weight. Comparing the weight at

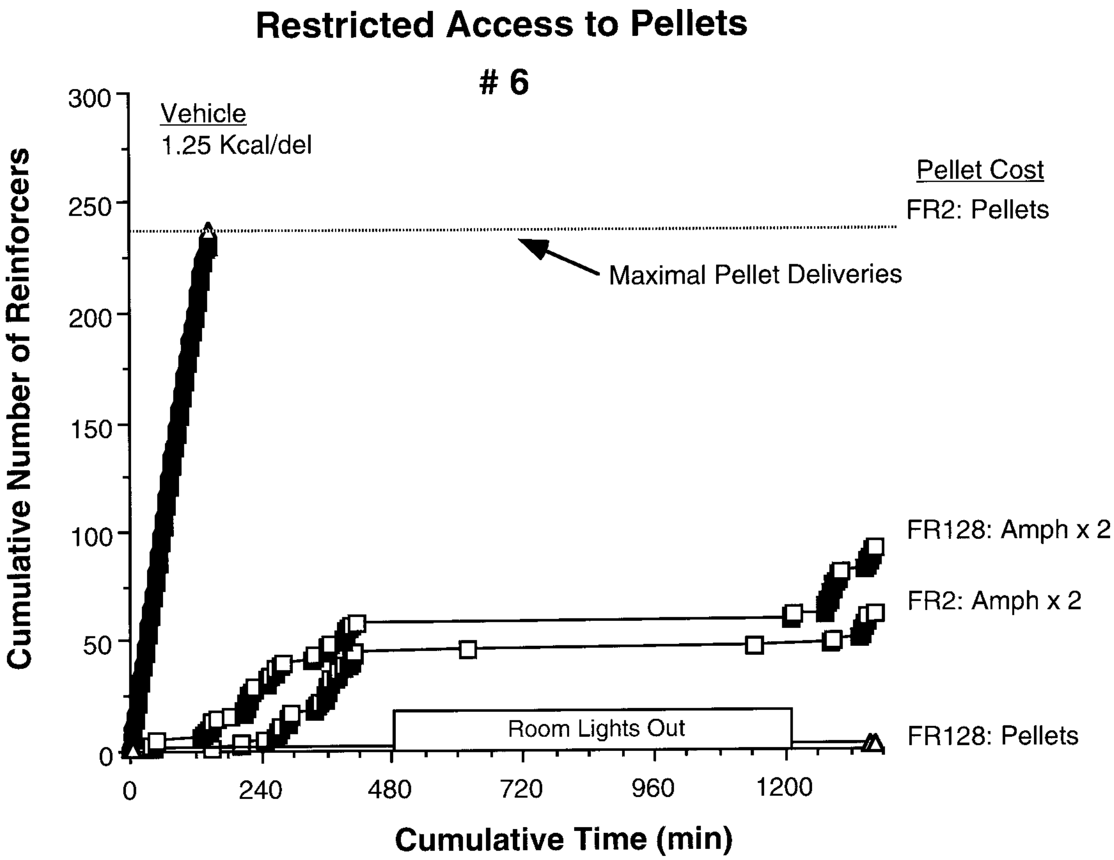


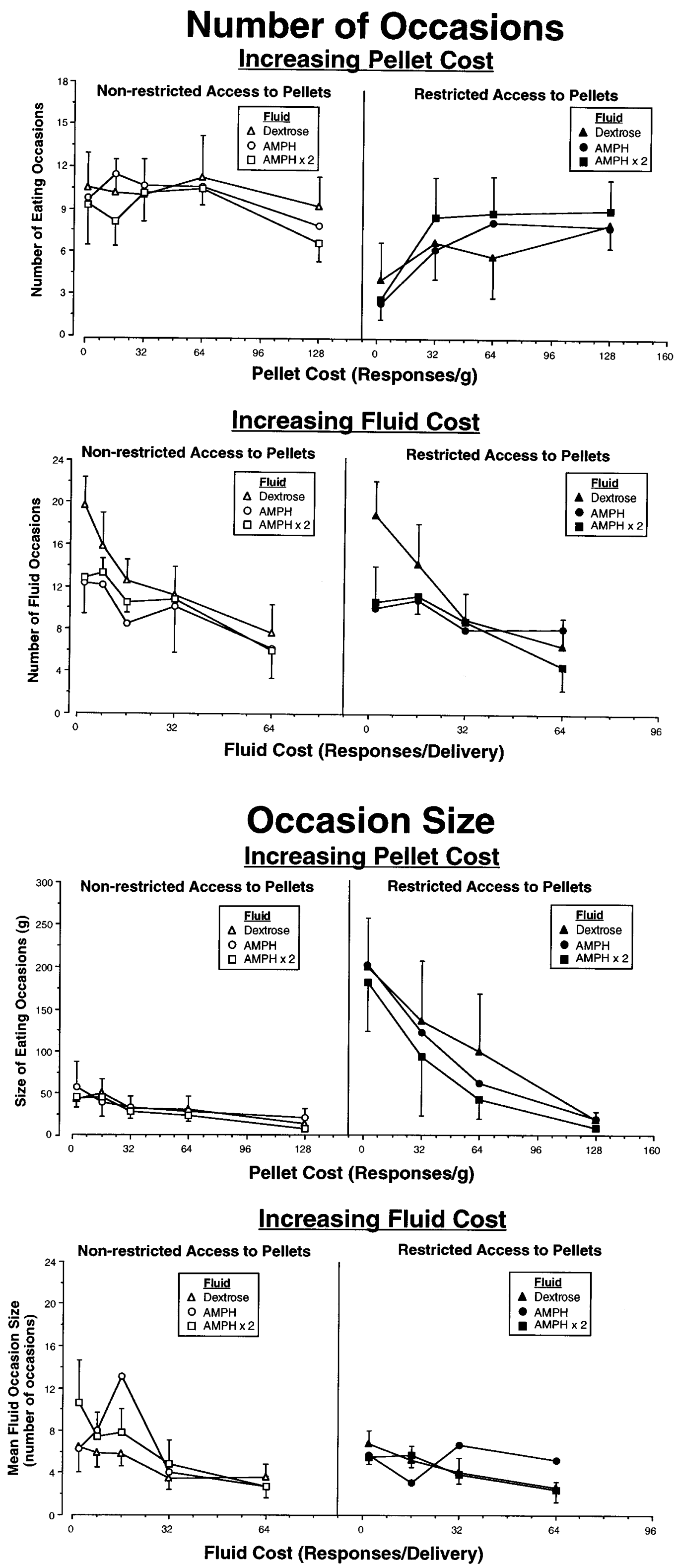
Fig. 8. Cumulative number of pellet and amphetamine deliveries when pellets were available at minimum (FR 2) and maximum cost (responses per delivery) for Baboon 6 (FR 128) when access to pellets was restricted. Each symbol represents reinforcement, not a response.

the end of the study to the beginning of the restricted access period indicates that 2 baboons lost 0.1 kg, whereas the remaining 4 baboons actually gained weight during the restricted access condition. Thus, restricting baboons to 70% of their baseline pellet intake failed to reduce their body weights when they had concurrent access to solutions containing dextrose. Baboons derived only about 100 kcal per day (equivalent to 27 pellets) from fluid under both access conditions; increases in amphetamine intake, and corresponding increases in caloric intake, during pellet restriction were variable among baboons. Thus, increases in caloric intake derived from dextrose vehicle alone or amphetamine doses were not sufficient to make up for the difference in calories derived from pellets (decreases of 303 to 710 kcal per day or 82 to 192 pellets per day). In spite of this decrease in total daily caloric intake during the restricted access condition, baboons maintained stable weights under both access conditions.

DISCUSSION

Effect of Fluid Availability on Responding Maintained by Food Pellets

The purpose of the present study was to examine how responding for food pellets would be affected by the concurrent availability of an oral amphetamine solution, and how responding for fluid would be affected by the concurrent availability of food pellets. When baboons had nonrestricted access to pellets, self-administered amphetamine and dextrose vehicle significantly decreased total daily pellet intake when pellets were available at minimal cost. Increasing the response re-



Number of Occasions
Increasing Pellet Cost
Non-restricted Access to Pellets
Restricted Access to Pellets
Fluid
Dextrose
AMPH
AMPH x 2
Number of Eating Occasions
Pellet Cost (Responses/g)
Increasing Fluid Cost
Number of Fluid Occasions
Fluid Cost (Responses/Delivery)
Occasion Size
Increasing Pellet Cost
Size of Eating Occasions (g)
Pellet Cost (Responses/g)
Increasing Fluid Cost
Mean Fluid Occasion Size (number of occasions)
Fluid Cost (Responses/Delivery)

Table 3

Baboon weights (kg).

Baboon	Begin study	Begin restriction	Difference[a]	End restriction	Difference[b]
1	47.0	47.4	0.4	47.7	0.3
2	30.0	30.0	0.0	29.9	−0.1
3	26.6	23.3	−3.3	23.2	−0.1
4	26.9	27.5	0.6	27.9	0.4
5	24.4	28.0	3.6	28.3	0.3
6	32.4	31.0	−1.4	31.6	0.6
M	31.2	31.2	−0.0	31.4	0.2
SEM	3.7	3.7	1.0	3.8	0.1

[a] Difference between starting study weight and weight at beginning of pellet restriction.

[b] Difference between weight at beginning and end of pellet restriction.

quirement for pellets decreased pellet intake at a similar rate regardless of the available fluid. Increasing the response requirement for pellets tended to increase fluid intake, but in a variable manner among baboons so that there were no statistically significant increases in fluid intake. When access to pellets was restricted to 70% of the intake at minimal cost under nonrestricted conditions, increasing the response requirement for pellets decreased pellet intake at a significantly faster rate when the high amphetamine dose was available than when the other fluids were available. Increasing the cost for pellets also tended to increase intake of the high amphetamine dose ($p < .06$). Thus, amphetamine functioned as an economic substitute for pellets to a greater extent than did the dextrose vehicle, but only when total daily pellet intake was restricted.

Restricting access to pellets to 70% of baseline intake altered response output function without affecting body weight. The failure of this procedure to reduce body weight was not due to an increased caloric intake derived from vehicle or amphetamine solutions. Under restricted access conditions, pellet intake at minimal cost was identical under all four conditions (i.e., no alternative, dextrose, low amphetamine dose, high amphetamine dose), and baboons consumed almost all of their daily pellets during a single eating occasion at the beginning of a session; responding for fluid did not occur until after eating ceased.

Changes in the pattern of pellet and fluid intake as a consequence of increasing pellet cost were dependent upon baseline intake pattern. When access to pellets was not restricted, increasing the cost for pellets decreased pellet intake by decreasing the size of eating occasions without affecting the number of eating occasions. When access to pellets was restricted, increasing pellet cost decreased pellet intake both by decreasing the size of eating occasions and by increasing the number of eating occasions.

In a recent review, Bickel et al. (1995) summarized eight drug studies, using both nonhuman and human participants, that reported commodity substitution, as defined by an increase in consumption of the alternative when the cost for the primary commodity was increased. Only four of these studies used concurrently available nonidentical commodities, and unfortunately, the evidence for substitution was limited. Substitution was evident in only 1 of 4 rats in two of the studies (Carroll & Meisch, 1979; Samson, Tolliver, & Roehrs, 1983), and in the third study, the alternative commodity only produced a parallel downward shift in the intake curve of the original commodity (Carroll, 1987). The study that showed the most consistent substitution effect (3 of 4 rats) revealed an increase in ethanol self-administration when the cost of a concurrently available preferred sucrose solution was increased from FR 8 to FR 64 (Samson, Roehrs, & Tolliver, 1982). This effect was not replicated, however, in a later study when the cost for sucrose was increased

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Fig. 9. Mean number of eating occasions as a function of pellet cost and fluid type under both pellet-access conditions, mean number of drinking occasions as a function of pellet cost and fluid type under both pellet-access conditions, mean size of eating occasions as a function of pellet cost and fluid type under both pellet-access conditions, and mean size of drinking occasions as a function of pellet cost and fluid under both pellet-access conditions. Error bars, representing 1 *SEM,* are presented for the dextrose and high amphetamine dose only. An occasion began with the first response for a commodity and ended when there was a pause longer than 10 min between reinforcement and the initiation of responding under another FR.

gradually from FR 8 to FR 32, then to FR 64 (Samson et al., 1983), suggesting that the rate of change in the cost of one commodity affected substitution between commodities. Although too recent to have been included in the Bickel et al. (1995) review, Comer, Hunt, and Carroll (1994) reported that self-administered saccharin functioned as an economic substitute for smoked cocaine in rhesus monkeys. Thus, with the exception of data presented by Comer et al. (1994), substitution among nonidentical commodities has been difficult to observe.

There was a greater similarity between the two available commodities in the present study than in some of the previous drug studies because amphetamine was presented in a dilute dextrose vehicle containing about one third the calories of a food pellet. Although the energy content of the vehicle may have been a contributing factor, there is still evidence that amphetamine functioned as a substitute for pellets when access to pellets was restricted. The criterion for amphetamine substitution was based on comparisons to vehicle control data, not to data from conditions providing pellets without any alternative.

When access to pellets was restricted and the high-dose amphetamine was concurrently available, increasing pellet cost tended to increase high-dose amphetamine intake ($p <$ .06), and to decrease pellet intake at a faster rate than when the dextrose vehicle was available. Amphetamine is an effective anorectic drug (Foltin, 1993; Foltin et al., 1990), suggesting that the more rapid decrease in pellet intake reflected a direct effect of amphetamine in reducing food intake. Thus, the anorectic effects of amphetamine may play a role in determining its ability to function as an economic substitute for food.

The effects of amphetamine on behavior are often dependent upon rate of responding, with low-rate behavior increased and high-rate behavior decreased (i.e., rate dependency; Kelleher & Morse, 1968; McMillan, 1969). Because running response rates were similar across all pellet costs greater than FR 2, the greater decrease in pellet intake at higher pellet costs when amphetamine was concurrently available and access to pellets was restricted cannot be related to rate of responding for pellets. The greater decrease in pellet intake at higher pellet costs may also reflect an enhanced sensitivity of responding maintained under large fixed ratios to disruption. For example, responding by pigeons maintained by FR schedules of food delivery was more disrupted by low doses of the short-acting stimulant cocaine when the FR was large than when the FR was small (Hoffman, Branch, & Sizemore, 1987). A previous study from this laboratory provided no evidence, however, that responding of baboons maintained by food pellets under larger FR schedules was more sensitive to the effects of amphetamine (Foltin, 1993). In that study, increasing the cost for pellets decreased pellet intake, and the administration of six anorectic drugs, including *d*-amphetamine, produced parallel shifts downward in pellet intake at all response costs.

Effect of Pellet Availability on Responding Maintained by Fluid

Given the typically robust increases in drug self-administration as a result of body-weight reduction, an additional purpose of the present study was to evaluate the effect of body-weight reductions on responding maintained by amphetamine. However, the baboons did not lose weight when pellet intake was restricted to 70% of nonrestricted conditions. Clearly, adult male baboons differ from smaller laboratory animals in that body weight is more resistant to change.

Adding amphetamine to the vehicle solution decreased the number of fluid deliveries when fluid was available at minimal cost. Although most baboons consumed slightly more amphetamine each day when the higher amphetamine concentration was available, the number of actual fluid deliveries was usually reduced, indicating that the baboons' behavior was sensitive to the amphetamine concentration of the fluid. Although responding varied as a function of amphetamine concentration, the response-rate measure provided little evidence that oral amphetamine functioned as a reinforcer when the group data were analyzed. These results vary from other studies that have demonstrated the oral self-administration of amphetamine by laboratory animals (Carroll & Stotz, 1983; Kanarek & Marks-Kaufman, 1988; Kongyingyoes, Jänicke, & Coper, 1988).

Increasing the response cost for fluid decreased fluid intake by predominantly decreasing the number of drinking occasions and, under restricted-pellet access conditions, producing a small decrease in mean drinking occasion size. Increasing the response cost for the high amphetamine dose increased pellet intake when access to pellets was nonrestricted. Although the increase in pellet intake fulfills the definition of an economic substitute, this increase in pellet intake was more probably related to the decreasing anorectic effect of amphetamine as amphetamine consumption decreased.

Conclusions

When given nonrestricted concurrent access to food pellets and amphetamine, baboons self-administered sufficient amphetamine to decrease pellet intake. Increasing the response requirement for pellets decreased pellet intake at a similar rate regardless of the available fluid and increased fluid intake in a variable manner among baboons such that there were no statistically significant increases in fluid intake. There was minimal evidence that self-administered amphetamine could function as an economic substitute for food pellets when access to pellets was not restricted. In contrast, when access to pellets was restricted, increasing pellet cost decreased pellet intake and increased fluid intake more rapidly when the available fluid was the high amphetamine dose than when it was any of the other fluids. Thus, amphetamine was more effective as an economic substitute for pellets when access to pellets was restricted.

Although pellet restriction, without weight loss, increased amphetamine self-administration during at least one test phase for all baboons, this effect was variable and less robust than that observed in studies when food restriction decreased body weight (Carroll & Meisch, 1984).

Unfortunately, there are some limitations imposed by the current methodology that may affect the generality of the findings. (a) Amphetamine substitution for pellets may have been enhanced due to the caloric content of the vehicle. (b) Reducing the caloric content of the vehicle for 3 baboons under the restricted access condition clearly affected behavior. (c) These observations were based on 23-hr daily sessions, which have been rarely used in other studies. (d) Pellet restriction did not reduce body weight. (e) The data were collected in unusually large laboratory animals (three to six times the weight of a rhesus monkey; 100 times the weight of a rat). (f) Pellet restriction altered the topography of pellet and fluid intake such that nearly all pellets were consumed *before* any fluid consumption, resulting in behavior that appeared to be under a multiple schedule rather than a concurrent schedule. (g) Each FR value was examined for a predetermined 2 or 3 days, rather than using stability criteria to determine how long each cost was tested.

Clearly all research designs have limitations, and the present case, as noted above, is no exception. Some of the limitations would have been difficult to predict, such as the lack of weight loss, whereas others, such as the duration of each FR value, were inherent in the methodology. The decreases in responding for a commodity with increasing cost were reliable and demonstrable with only 2-day conditions. The brief testing of each FR value may have increased the variability, thus decreasing power. The design was selected because it provided parametric data in the same animals over a reasonable time frame. For example, increasing the duration of each FR value to 4 days would have increased the study duration to 2 years (rather than 1 year).

The present results clearly indicate that substitution between commodities with minimal commonalities can be studied under controlled laboratory conditions, and is dependent upon reinforcement schedule and commodity restrictions. The results also indicate the difficulty in interpreting reinforcer interactions when the pharmacological effects of one commodity (e.g., the anorectic and rate-dependent effects of amphetamine) may alter consumption of the second commodity independent of cost considerations. It is of special interest to examine interactions among dissimilar commodities involving drugs of abuse and other responses in order to identify behavioral variables that affect drug self-administration.

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